The diet of a facultative scavenger, the wolverine (*Gulo gulo*), after recolonization of wolf (*Canis lupus*) in southern Norway

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Master of Science thesis

2006

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Wolverine project

Preface

This study was conducted under joint supervision from NINA and the University of Oslo. The study is a part of a larger study at NINA and the objective is to obtain a greater insight in the ecological role of the wolverine and how they are adapting to an ecosystem in change.
Arild Landa was the official supervisor at NINA, but PhD student Jiska van Djik performed most of the supervision during the first period. Atle Mysterud was the formal supervisor at the University of Oslo and performed most of the supervision on statistical analysis and writing.
I thank Jiska van Djik and Arild Landa for giving me this thesis. I also thank them for believing in me and letting me have an oral presentation at the 1st International Symposium on Wolverine Research and Management in June 2005.
I also thank Atle Mysterud for stepping in and taking me as a student in May, 2006. My study benefited greatly from his participation. Atle always had time for me, replied to every e-mail with incredible promptness, and was there with positive words and encouragement! Thank you! I thank Harald Steen for the supervision during the first period of this process. I also thank Erling J. Solberg and John Linnell at NINA for contributing to make my time there a great one.
I thank Earl Becker for reading my thesis and commenting on my English, Anne Kristina Ehrlinger and Irja Ida Ratikainen for reading and commenting on my thesis and for always having positive a positive attitude.
I thank my family for always being there for me, and my nephew Mathias for bringing so much light and joy into my life. I couldn't have done this without them!

Line,

Blindern, October 30th 2006

To my father

Tor Gustavsen

1935-2004

Thank you for everything.

Abstract

In the recent decades large carnivores have started to recolonize former occupied areas in North America and in Europe. Increases in predator population sizes can affect the whole ecosystem functioning, but little work has been done on this area in Europe, especially when it comes to how scavengers are affected. The wolverine (*Gulo gulo*) is both a predator and a scavenger, and switches between this two roles. In this study, the wolverines' diet was investigated in southern Norway based on scats found during winters in 2002 to 2004. My aim was to find out if recolonizing wolves (*Canis lupus*) might have changed the wolverines' diet. I also investigated if there were sexual differences in diet in the wolverine population, and if diet varied annually and according to habitat. Moose (*Alces alces*) stood for 42.3% of the diet, reindeer (*Rangifer tarandus*) for 29.1% and small game (mainly rodents) for 29.7%. There was a broad structure in the data, and two axes were identified by Principal Component Analysis. The first axis (explaining 49.7% of the variation) was positively correlated with frequency of small game. The second axis (cumulative variance explained 91.7%) was strongly correlated with frequency of occurrence of small game that had been eaten and negatively correlated with the occurrence of both reindeer and (partly) moose that had been eaten. Before the re-colonization of wolves and recent increases in moose density, reindeer was the most important prey for the wolverine, but during the period of this study moose was the most important food source for the overall population. As predicted, the wolverines ate more moose inside than outside of wolf territories, indicating that wolves have increased the availability of moose carrions for wolverines. Females ate more small game than males, and males ate more big game than females. There were also annual variations in the diet but there were no marked variations between the different habitats apart from altitude. This study highlights how recolonization of carnivores can affect the diet of a scavenger by increasing the amount of carrions that are available, and thus change ecosystem functioning in northern habitats.

Contents

1. Introduction

Ecosystems consist of food webs, including both producers and consumers at different trophic levels. In terrestrial ecosystems the producers are plants and the consumers are herbivores and carnivores. Population ecologist working with mammals debate whether ecosystems are mainly regulated by top-down or bottom-up processes (Sinclair, 2003). In the absence of predators and/or parasites bottom-up processes can regulate populations (Sinclair, 2003), but this may even occur in the presence of large carnivores depending also on limitation by abiotic factors (Vucetich & Peterson, 2003). The four main conditions that predict when top-down regulation could occur are body size, high diversity systems, migration and low-diversity ecosystems (Sinclair, 2003). These issues have gained new relevance given the recolonization of large carnivores in many parts of North America and Europe in recent decades (Berger *et al.*, 2001). Little attention has been paid to the influence of top predators on fellow guild members (Wilmers *et al.*, 2003), such as scavengers. After reintroduction of grey wolf (*Canis lupus*) to the Yellowstone National Park started in 1995 (Smith *et al.*, 2004), Wilmers *et al.* (2003) found that the supply of elk (*Cervus elaphus*) carrion had turned from a pulsed resource at the end of severe winters before the reintroduction of wolves to a more constant resource throughout the winter and the whole year. This leads to a more constant food source for scavengers.

Scandinavia is a typical example of this new situation in the terrestrial ecosystems of Europe. In recent decades, both brown bears (*Ursus arctos*) (Swenson *et al.*, 1998; Swenson *et al.*, 1995) and wolves (Wabakken *et al.*, 2001b) have greatly increased their distribution and population size. So far, there have been few studies examining how this may affect ecosystem functioning, and how large carnivores may affect the diet of scavengers. In Scandinavia, the wolverine (*Gulo gulo*) is mainly a scavenger of large ungulates (Haglund, 1966). Wolverine are the largest terrestrial mustelid and one of Norway's four large carnivores along with brown bear, wolf and lynx (*Lynx lynx*) (Landa & Skogland, 1995). The wolverine population in Norway fell to critically low numbers in the 1960 due to hunting (Landa *et al.*, 1999), and this lead to wolverine protection in southern and northern Norway in 1973 and 1982, respectively (Landa *et al.*, 1999). The protection resulted in an increase in the number of wolverines and recolonization of unoccupied historical wolverine range.
The wolverine is polyphagous, so it can switch between different food sources as some prey become scarce (Landa *et al.*, 1997b). It is likely that the diet of wolverines that have access to

carrion will contain different species or more of certain species than the diet of wolverines that don't have access to carrions. Before the main period of recolonization of wolves in Norway, Haglund (1966), Myhre *et al* (1975) and Landa *et al*. (1997b) found that reindeer (*Rangifer tarandus*) was the most important food during winter in Sweden and Norway. However, hares (*Lepus timidus*), ptarmigan (*Lagopus sp*.) and small rodents may also be important food at this time of year (Myhre *et al.*, 1975), and might be the most important food during summer (Landa *et al.*, 1997b; Magoun, 1987; Myrberget & Sørumgård, 1979). Larger animals in the wolverine's diet are most likely eaten as carrion (Magoun, 1987), but the wolverine can hunt domestic sheep (*Ovis aries*) (Olestad, 1945), semi-domestic reindeer, and on rare occasions even moose (*Alces alces*) (Haglund, 1974). The amount of prey might affect predators hunting behaviour (Landa *et al.*, 1999), and Lugton (1993) discovered that lamb predation by red fox (*Vulpes vulpes*) was more severe when the preferred food source was scarce.

To investigate the importance of other predators, mainly wolf, on the wolverine's diet I studied the diet composition through faecal analysis. Wolverine faecal samples were collected in southern Norway in regions with and without wolves. I tested the following hypotheses:

1. *The carrion availability hypothesis.* "The diet of wolverines depends on the local availability of carrion, so the wolverine diet can be related to the presence of wolves by larger amounts of big game in their diet". It is known that the wolverine scavenge on kills from other large carnivores (Landa *et al.*, 1997b), but it is not known how much of the wolverines diet is affected by the presence wolves. Moose will most likely be eaten as carrion (Myhre *et al.*, 1975), and thus I expect that the diet of wolverines living in the same area as wolves will consist more of big game, indicative of scavenging, than the diet of wolverines in areas without wolves.

2. *The sexual segregation hypothesis.* "The diet of female wolverines is expected to be based less on scavenging than that of male". Mechanisms for such a pattern may be that the smaller home range size of female wolverines, due to their dependent offspring, causes them to encountering fewer carcasses. Radio-collared adult males in the Snøhetta area used on average a minimum of 763 km^2 during a year, while adult females only used 335 km^2 (Landa *et al.*, 1997a). I expect to find more traces of large prey, such as moose in the faeces from males than from females. Due to this, I would expect that females are more dependent on smaller prey such as rodents and birds.

3. *The habitat hypothesis.* "The wolverines' diet depends on prey availability within its home range". I expect that moose is more common in the forest and at low altitude, (Semb-Johansson, 1990a)and that the presence of reindeer is more restricted to high altitude and absence of forest (Semb-Johansson, 1990a). Rodent species, however, are present in all habitats and altitudes (except at very high altitudes). Two different sub populations have been identified in southern Norway (Flagstad *et al.*, 2004; Walker *et al.*, 2001). The south-west (SS) population lives mainly in mountain areas and the north-east (NN) population lives more in the mountain forest and in forest areas. I will therefore expect that the NN population will have more moose in its diet because it will have greater access to moose than the SS population.

4. *The annual variation hypothesis.* "The diet of the wolverine will vary from year to year". The wolverines hunting success is largely dominated by the snow conditions during wintertime (Wilson, 1982). The wolverine can walk better in deep snow conditions than its prey which sinks deeper down in the snow (Haglund, 1966). This makes it easier for the wolverine to catch large prey such as reindeer and moose (Ewer, 1973). Also, mortality among ungulates is higher during severe snow conditions (Wilmers *et al.*, 2003). I expect to find yearly variation in the amount of big game eaten, and that it will be correlated with snow depth. I expect diet to contain more big game in years with high snowfall, but cannot test this directly due to a low number of years.

2. Materials and methods

2.1 Study area

The study area encompasses much of the current distribution range of wolverine in Southern-Norway. Today the wolverine lives mainly in the mountain areas in central South Norway and along the Norwegian-Swedish border from Hedmark County (south-east Norway) and up north including Finnmark County (Landa *et al.*, 1999). The whole study area consists of 63 municipalities, where Røyrvik and Namskogan in Nord-Trøndelag County are the most northern municipalities and Kvinesdal in Aust-Agder County is the most southern municipality. In the Snøhetta area in Dovre municipality wolverines live without other large carnivores, in the Lierne municipality they live with bears and in Hedmark County they live with wolf, lynx and a few bears. Figure 1 indicates wolverine distribution relative to presence or absence of wolves.

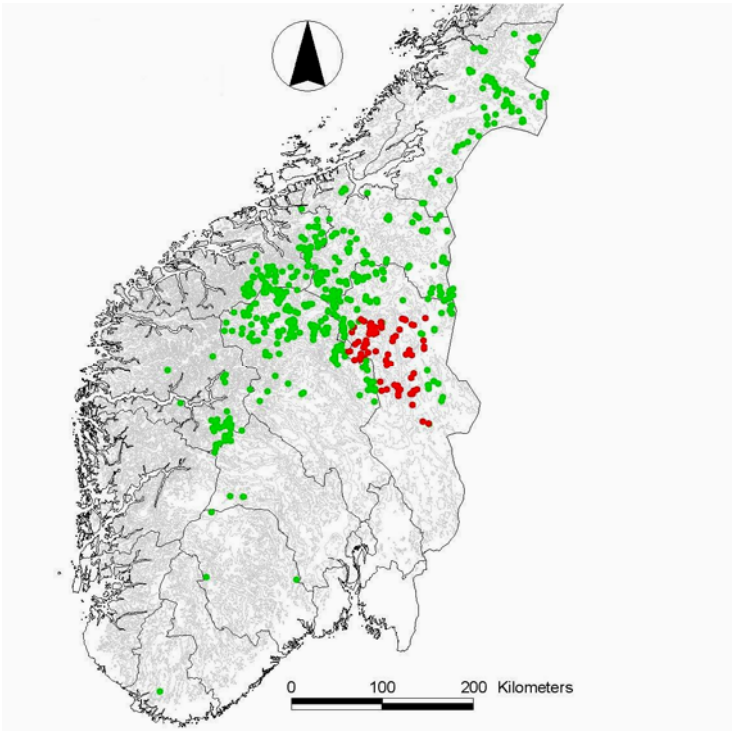

Fig. 1 The study area covers much of the alpine areas of southern Norway, extending also into the boreal forest. Red dots are places where the wolverine lives with wolf and green dots marks the places where the wolverine lives with absence of wolf. The areas with both wolf and wolverine are all located in Hedmark County.

Through registration of cubs it has been estimated that the Scandinavian wolverine population is around 595 (SE = 69) individuals (1998-2000), (Flagstad *et al.*, 2004). Through DNA analysis of faeces the population in Southern Norway was estimated to be around 90 individuals (95% CI: 82-103) in 2005 (Flagstad *et al.*, 2005).

The study area is very large, and it varies considerable in vegetation, topography, climate and in what other species that are present. In the west there is a costal climate, in the middle an alpine climate and in the east a more continental climate. The altitude varies from sea level to over 1800 m. a.s.l. The area can be divided into mountain and open moors, birch (*Betula sp*.) forest, coniferous forest, agricultural areas and city areas (Moen, 1998). The timber line is around 1000 meters above sea level, and the wolverine seems to avoid forest during summer and tundra during the winter (Pasitschniak-Arts & Larivière, 1995). The vegetation zones in southern Norway are south arctic zone, north boreal zone, middle boreal zone, south boreal zone, and boreo-nemoral zone (Abrahamsen *et al.*, 1977). The alpine zone lies in the mountain areas in the middle of south Norway, and the north boreal zone exists in large areas in the east. The middle boreal zone exists in the south-east of Southern Norway, at the south coast, and in Trøndelag County. The South boreal zone exists a bit into the country and along the coast of Trøndelag, and the boreo-nemoral zone runs like a belt along the cost of South Norway and with a few scattered incidences in Trøndelag.

The most common potential prey items are moose, wild and semi-domestic reindeer, hare and small rodents. Moose is distributed almost over the entire area, except for some municipialities on the west coast, below the tree limit, and roe deer (*Capreolus capreolus*) have almost the same distribution (Andersen *et al.*, 2004; Semb-Johansson, 1990a). Wild reindeer live in the mountain and in the birch belt found mainly in the South-Central Norwegian Mountain Plateaus (Semb-Johansson, 1990a) and semi-domestic reindeer are distributed in the north eastern part of Hedmark County and in the counties of South Trøndelag and North Trøndelag. Mountain grouse (*Lagopus mutus*) and lemming (*Lemmus lemmus*) both live in mountainous areas (Hogstad & Semb-Johansson, 1992; Semb-Johansson, 1990b). Wolves are distributed mainly in Hedmark County (Wabakken *et al.*, 2001b).

2.2 Sampling of wolverine scats

The sampling of 908 wolverine scats was conducted between 2001 to 2004 during late winter season in Southern Norway as part of the national wolverine monitoring program. The sampling was administered by The Norwegian Nature Inspectorate (“Statens naturoppsyn”,

SNO). The GPS locations were noted so that spatial covariates could be accurately determined. After collection the scats were sent to Uppsala, Sweden, for DNA analysis, and the remaining part was divided in two equal parts where one part was used in diet analysis, and the other part was kept for storage.

2.3 Dietary analysis

To determine the diet composition each scat was washed in a sieve (0.5 mm) until the water was clear. I visually separated the different remaining items in the scat into hair, feathers, and other identifiable and unidentifiable items. The different items were dried in a drying oven at 45˚C for 48 hours. The hairs were identified to species level, except for small rodents and insectivores, by using a hair atlas (Brunner & Coman, 1974), identification key on Norwegian Cervids (Birkeland *et al.*, 1972), reference material, and by looking at the hair structure with a microscope. Jaws in the "rodent bones" category were identified to the finest taxonomic level possible, and identified by their length and teeth (Gaffrey, 1961; Mohr, 1954). Bones were classified as bird bones if they were hollow, and feathers were identified by looking at their barbules with a microscope. Of the 908 samples, 815 could be used to calculate the frequency of occurrence, of dietary items. Only 10 samples had to be removed because they didn't contain any hairs or feathers, and some other samples had to be removed because they didn't contain anything after rinsing. Other samples had to be removed because they did not originate from wolverine. To calculate the volume of the sample I followed the method of Grosse *et al.* (2003), by using an superimposed grid, and visually estimate the volumes. The frequency of occurrence (F_i) was calculated following Berducou *et al.* (1983):

$$F_i(\%) = \frac{n_i}{N} \times 100$$

where N is the total number of faecal samples and n the number of samples which contained remains from the i^{th} species. The frequency of occurrence of all items in the scats is listed in appendix table 1.

One potential data error would arise if hairs had been misidentified. This is possible because the method is based upon identification solely by humans. The hair atlas is based upon whole and perfect hairs that haven't gone through a digestive system, but in reality most of the hairs are only present as fragments. Nevertheless, this is regarded as less important. However, with the method I used, there was also a quite large amount of unknown hair, which may bias estimates to an unknown extent. The samples also contained so much hair that it was impossible to look at every hair in the microscope. I tried to identify all the hairs that looked

different from each other. So, there is a possibility that not all the species in a sample were identified, but it should only be very few and small hairs. Since I have used the same method on every sample, this is nevertheless not likely to affect the testing of the hypotheses, just the absolute numbers.

2.4 DNA analysis

All the scats were sent to Uppsala, Sweden, for DNA analysis using microsatelite markers (Flagstad *et al.*, 2002). This was used to verify that the scat was from wolverine, as well as to determine sex, individual identification and genetic sub-population. Samples that were identical in ten loci and represented the same sex, were classified as representatives for the same individual (Flagstad *et al.*, 2002). The individual's genotype was grouped either to the north-east (NN) population or the south-west (SS) population. The DNA analysis revealed that four samples belonged to a hybrid between the two different sub-populations, and they were removed in subsequent analysis.

2.5 Other covariates

The GPS position for each scat was noted during collection of the scat (see above), and this made it possible to retrieve more exact information about the position. An area was classified as wolf territory if it was a territory or a wolf couple/reproduction there in the period from 2000 to 2003 (Wabakken *et al.*, 2004; Wabakken *et al.*, 2001a, , 2002). The habitat types were classified using the AVHRR land cover image, and divided into forest, shrub land and tundra (United States Geological Survey, 2005), and altitude were classified as above or below 1000 meters of altitude (Norwegian State Mapping Authority, 2005). The categories "reindeer harvested" and "moose harvested" are the number of reindeer and moose shot in the county during the previous hunting season (autumn) of when the scat was found, divided by the area of the county (Statistic Norway, 2000-2003).

2.6 ***Statistical analyses***

A total of 801 scats yielded information to calculate the percentage of occurrence of different dietary items used in the statistical analysis. Lynx presence was excluded from the analysis because lynx are present in most of the study area, killing mainly roe deer and very rarely moose and reindeer. Bear presence was not considered due to few samples from the areas with bear.

Based on an initial screening of the data and what constituted the most important dietary items, I merged small mammals (including hare) and birds together as "small game", and I merged moose, reindeer, roe deer and sheep together as "big game". Only reindeer and moose among ungulates were important enough in the diet to warrant a more detailed analysis. I therefore had four response variables, frequency of small game, moose, reindeer, and big game in the diet. I first explored the relationship between amount of small game, moose and reindeer in the diet with Principal Component Analysis, before analysing each response variable separately. For these separate analyses of single or grouped dietary items, potential covariates were year (categorical; 2001-2004), gender (female [F], male [M], unknown [U]), genetic population (northeast [NN], southwest [SS], unknown [UU]), habitat (forest, shrub land, tundra), altitude (above or below 1000 m), reindeer shot per km^2, moose shot per km^2 and wolf territory (yes or no).

To find a model that fitted these data, I first tried ordinary linear models, with the response variable (percentage data) transformed by using a standard arcsin-squareroot transformation. However, standard diagnostics tools suggested a fairly poor model fit. I then tried generalized linear models, first using a poisson distribution, but also here the fit of the models were poor. I then tried a logistic regression model, after first classifying data into little/much of the three main dietary items. Neither of these approaches resulted in improvements in model fit, but in all models, the same main factors appeared as important. I therefore returned to linear models in the model selection (see below) even if the fit was not optimal. In order to improve fit and robustness I bootstrapped the final model (Efron & Tibshirani, 1993). Bootstrap uses the data (residuals) to make a distribution, so that the assumption of normality and single influential values are no longer an issue (Efron *et al.*, 1993). A parameteric bootstrap with 1000 iterations was used.

Model selection was conducted by using automatic stepwise model selection by exact Akaike Information Criterion (AIC). Based on the AIC, models can be ranked from best to worst (Burnham & Anderson, 2004). The most parsimonious (best) model is the one with the lowest AIC value, representing a compromise between most variance explained by the model and the smallest number of variables (Burnham *et al.*, 2004).

All analyses were conducted in S-Plus version 6.2 and the significance was assessed by that the 95% confidence intervals should not overlap zero.

3. Results

During the 2001-2004 period, moose (42%) were the most important food source for wolverine (n = 801) in southern Norway, followed by reindeer (29%) and small mammals (23%). Both roe deer and sheep were very rare in the diet, 1% and 3% respectively (table 1). The PCA analysis identified two axes containing some broad structure in the data (fig. 2). The first axis explained 49.7% of the variation in the diet, and cumulative variance explained increased to 91.7% when the second axis was included. The first axis was positively correlated with frequency of occurrence of reindeer, negatively correlated with moose, while it was uncorrelated with occurrence of small game. Thus, there is a negative correlation between moose and reindeer in the scats, which is sound because moose mainly live in forested areas while reindeer lives in alpine habitat. The second axis is strongly correlated with frequency of occurrence of small game that has been eaten and negatively correlated with the occurrence of both reindeer and (partly) moose that has been eaten (fig. 2). So, when the wolverines ate a lot of small game they did not eat moose or reindeer.

Table 1. Frequency of occurrence of different prey in the diet of wolverine in the period 2001-2004, based on hairs and feathers found in scats.

Dietary item	Male	Female	Unknown	Total
Big game	80.6	73.1	70.4	73.9
Reindeer	32.5	27.3	28.50	29.10
Moose	46.6	43.9	56.7	42.3
Roe deer	1.9	0.4	2.60	1.40
Sheep	1.5	3.6	4.10	3.30
Small game	11.2	20.2	48.1	29.70
Hare	2.4	4.0	7.60	5.10
Small mammals	8.3	14.20	39.3	23.40
Birds	1.5	3.20	12.0	6.50

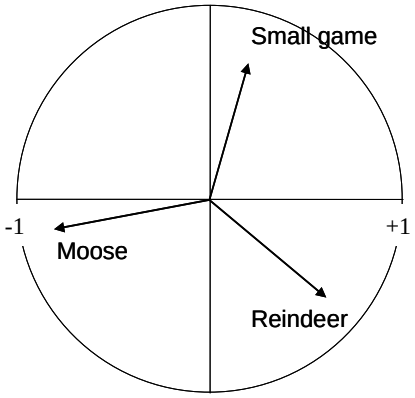

Fig. 2. Principal Component Analysis of the main dietary items of wolverine in southern Norway during 2001-2004. The first axis explained 49.7% of the variation, while the cumulative variation explained increased to 91.7% when the second axis was included. The first axis picked up that moose and reindeer was negatively correlated in the diet, while the second axis picked up that small game and big game was negatively correlated.

3.1 Big game

The final model contained the variables gender, year, wolf territory, altitude, and genetic population (table 2). It also contained the interactions between year and altitude and between height and genetic population. Big game was significantly more frequent in the diet inside wolf territories than outside, and this is consistent with the carrion availability hypothesis. The diet of males contained a significantly higher frequency of large game than females (fig. 3), and this is consistent with the sexual segregation hypothesis. In 2002 the frequency of big game in the diet was less than in 2001, but in 2003 big game was more frequent than in 2001. In 2002 big game was less frequent under 1000 m than above 1000 m in 2001, but in 2004 it was more frequent under 1000 m than above in 2001. The genetic population SS had less big game in their diet under 1000 m than population NN did above 1000 m.

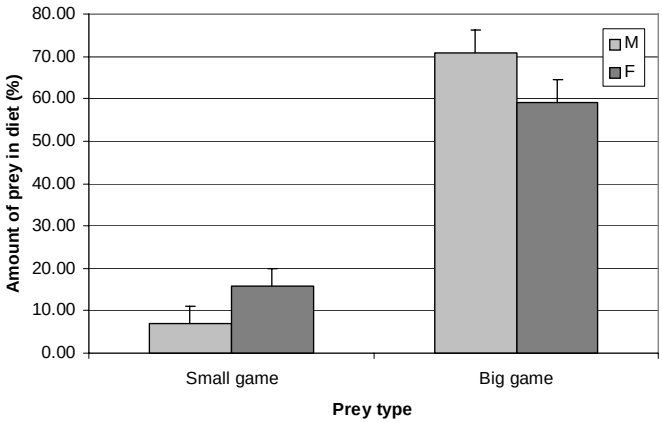

Fig. 3. Predicted amount (+ Std. Error) of small game and big game eaten by females and males in 2001 under 1000 m a.s.l, and outside wolf territory. Females had a significant higher frequency of small game than males in their diet during the whole study period, and males had higher frequency of big game than females in the diet. Predicted values are based on estimates from table 2.

3.2 Small game

The final model contained the variables gender, year, wolf territory and altitude, and the interactions between year and altitude (table 2). Small game was more frequent in the wolverines' diet outside than inside the wolf territories (fig. 4), which is consistent with the carrion availability hypothesis. Small game was also significantly less frequent in the diet of males than in that of females (fig. 3), providing support to the sexual segregation hypothesis. The unknown samples contained significantly more small game than both the male and female samples, suggesting a difficulty in the sexing of the animals related to diet. Small game was much more frequent in the diet in 2002 and somewhat less in 2003 compared to 2001. Even though the interaction between altitude and year (2002 vs. 2001) came out as significant, the frequency of small game in the diet was consistent higher below than above 1000 m a.s.l. for all years.

3.3 Moose

The best model based on the AIC criterion contained the variables genetic population, year and wolf territory (table 2). The frequency of moose in the diet was higher inside than outside wolf territories (fig. 4), consistent with the carrion availability hypothesis. This result remained also after controlling for moose density as assessed by the harvesting record (mean = -0.26559, SE=0.08228). The SS population had a significantly lower frequency of moose in their diet than the NN population did. This is consistent with the habitat hypothesis. In 2003 wolverines diet had a significantly higher frequency of moose than in 2001.

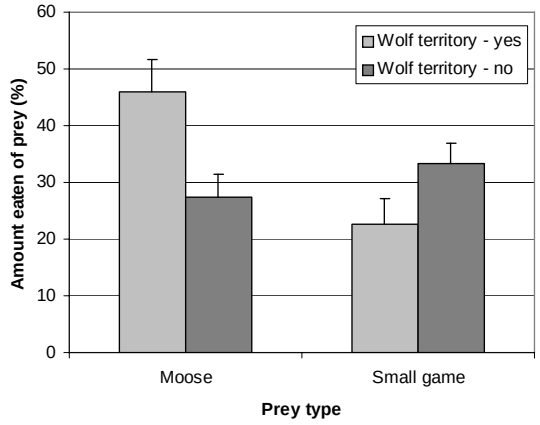

Fig. 4. Predicted amount (+ Std. Error) of moose and small game eaten by wolverine outside and inside of wolf territories in southern Norway in 2002. A significantly higher frequency of moose was found in the diet inside of wolf territories during the whole study period, and the opposite was true for small game. Predicted values are based on estimates from table 2.

3.4 Reindeer

The best model based on the AIC criterion contained the variables altitude, habitat and year, and the interaction between altitude and year (table 2). The frequency of reindeer in the diet was significantly lower below than above 1000 m a.s.l. (fig. 5). This provides support to the habitat hypothesis since reindeer are absent in the lower habitats, but the effect varied between years. In 2003 and 2004 the frequency of reindeer in the diet was significantly lower than in 2001.

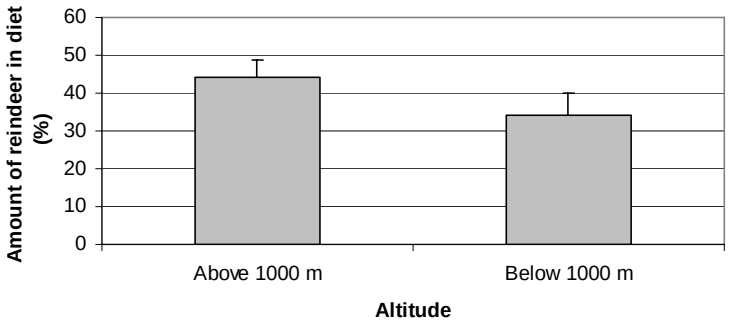

Fig. 5. Predicted amount (+ Std. Error) of reindeer eaten by wolverine in 2001 on the tundra. The frequency of reindeer in the diet was significant higher above than below 1000 m a.s.l during the whole study period.

Table 2. The results are from the bootstrap analysis of the best model as judged from the AIC. Variables with an estimated effect that does not include zero (hence termed significant) are marked by a star.

Reindeer	Estimate	SE	Lower 95% CI	Upper 95% CI	
Intercept	0.736	0.097	0.931	0.542	
Altitude (below vs. above 1000 m)	-0.370	0.130	-0.110	-0.631	*
Habitat (Shrub land vs. Forest)	-0.117	0.059	0.001	-0.236	
Habitat (Tundra vs. Forest)	0.029	0.070	0.168	-0.110	
Year (2002 vs. 2001)	-0.155	0.111	0.068	-0.378	
Year (2003 vs. 2001)	-0.223	0.106	-0.011	-0.436	*
Year (2004 vs. 2001)	-0.280	0.106	-0.069	-0.492	*
Altitude:year (2002 vs. 2001)	0.005	0.162	0.328	-0.319	
Altitude:year (2003 vs. 2001)	0.183	0.154	0.490	-0.124	
Altitude:year (2004 vs. 2001)	0.495	0.156	0.807	0.184	*
Moose					
Intercept	0.983	0.105	1.194	0.772	
Geneticpop (SS vs. NN)	-0.197	0.070	-0.057	-0.337	*
Geneticpop (UU vs. NN)	-0.337	0.069	-0.198	-0.475	*
Year (2002 vs. 2001)	-0.060	0.085	0.111	-0.231	
Year (2003 vs. 2001)	0.216	0.083	0.381	0.050	*
Year (2004 vs. 2001)	0.042	0.084	0.211	-0.127	
Wolfterritory (yes [ja] vs. no [nei])	-0.294	0.076	-0.142	-0.447	*
Small game					
Intercept	0.216	0.031	0.277	0.155	
Gender (M vs. F)	-0.064	0.024	-0.015	-0.113	*
Gender (U vs. F)	0.116	0.013	0.141	0.091	*
Year (2002 vs. 2001)	0.123	0.033	0.188	0.058	*
Year (2003 vs. 2001)	-0.040	0.015	-0.010	-0.071	*
Year (2004 vs. 2001)	-0.021	0.011	0.000	-0.042	
Wolfterritory (ja [yes] vs. nei [no])	0.091	0.029	0.148	0.034	*
Altitude (below vs. above 1000 m)	0.059	0.020	0.100	0.019	*
Altitude:year (2002 vs. 2001)	0.070	0.032	0.134	0.007	*
Altitude:year (2003 vs. 2001)	-0.032	0.015	-0.001	-0.063	*
Altitude:year (2004 vs. 2001)	-0.024	0.010	-0.004	-0.045	*
Big game					
Intercept	1.139	0.040	1.220	1.058	
Gender (M vs. F)	0.092	0.030	0.152	0.033	*
Gender (U vs. F)	0.256	0.224	0.704	-0.191	
Year (2002 vs. 2001)	-0.085	0.040	-0.004	-0.166	*
Year (2003 vs. 2001)	0.068	0.021	0.110	0.027	*
Year (2004 vs. 2001)	0.011	0.014	0.038	-0.017	
Wolf territory (ja [yes] vs. nei [no])	-0.105	0.037	-0.032	-0.179	*
Altitude(below vs. above 1000 m)	-0.051	0.031	0.011	-0.113	
Geneticpop (SS vs. NN)	-0.033	0.038	0.044	-0.110	
Geneticpop (UU vs. NN)	-0.334	0.223	0.113	-0.780	
Altitude:year (2002 vs. 2001)	-0.091	0.041	-0.010	-0.173	*
Altitude:year (2003 vs. 2001)	0.011	0.019	0.048	-0.027	
Altitude:year (2004 vs. 2001)	0.051	0.013	0.077	0.024	*
Altitude:geneticpop (SS vs. NN)	-0.078	0.038	-0.003	-0.153	*
Altitude:geneticpop (UU vs. NN)	0.001	0.018	0.036	-0.034	

4. Discussion

I analysed the winter diet of the wolverine in southern Norway including the area where wolves have recolonized. The two previous studies conducted on the wolverines diet during winter in Norway has reported that reindeer was the most important prey (Landa *et al.*, 1997b; Myhre *et al.*, 1975). In my study, however, I found that moose was the most important prey followed by reindeer and small mammals as measured by frequency of occurrence in their faeces. The study by Myhre *et al.* (1975) was conducted before wolves resettled and recent increases in moose density in Norway, and the one by Landa *et al.* (1997b) were conducted in the Snøhetta area, an area without wolves and in alpine habitat with little moose. As predicted by the carrion availability hypothesis, I found that the wolverine ate more moose and less small game within wolf territories than in areas without wolves, suggesting that wolf recolonization can induce a diet shift of scavengers such as the wolverine. Further, as predicted in the sexual segregation hypothesis, males ate more big game and less small game than females. There was also variation in diet between years. The low occurrence of sheep remains in the wolverine diet is not surprising, since data derive mainly from winter, and sheep in the Norway only graze on mountain pastures from June to the beginning of September. So the small amount of sheep in the wolverine's diet was likely from stored reserves.

4.1 Scavenging vs. predation - the carrion availability hypothesis (H1)

Wolverines are classified as a generalist that both scavenges and predates, and which switches between these two modes depending on what is the most profitable tactic (Haglund, 1966). When there are a lot of carcasses available the wolverine should prefer to scavenge. Scavenging does not require the energy expenditures necessary for hunting and killing prey, and at the same time reduces the risk of injury during attempts to capture large prey (Bauer *et al.*, 2005). The disadvantage of scavenging is the risk that the most valuable parts of the carcass already have been eaten. There is also a risk of being killed by wolves when scavenging on a wolf killed carcase. There are several observations of wolves killing wolverines (Boles, 1977; Krebs *et al.*, 2004). So during times when the conditions for hunting are good, the wolverine should trade carcass remains of lower energetic value for higher value organ and large muscle tissue on a fresh carcass that must be obtained at some cost (Wilmers *et al.*, 2003). When the hunting conditions are poor, looking for carrion or to use cached food

should be beneficial. So in areas with other carnivores, such as the wolf, the wolverine should have a larger opportunity to find carrions and should eat greater amounts of big game. My study finds this to be true of Norwegian wolverine. The wolverine ate significantly more moose inside active wolf range than outside. Since moose is most of the time eaten as carrion it is logical that the wolverine find more carrion of moose in areas with wolf territories. In a study by Myhre and Myrberget (1975) moose stood for only 7.9% of the diet, compared to the large proportions (x%) found in this study. I attribute this difference to wolf recolonization increasing the abundance of carrions available in certain areas of southern Norway. Clearly also, moose is more abundant today than in 1975 (Solberg *et al.*, 2006). I also found that the frequency of small game in the diet was significantly lower inside wolf territories than outside. This supports my hypothesis that when high value carcasses available the wolverine should trade off small game for big carcasses such as moose.

4.2 Sexual segregation (H2)

Several hypothesis have been proposed to explain why sexual segregation (sexual differences in space use, habitat use or diet) exists in vertebrates (Ruckstuhl & Neuhaus, 2005). There are many cases of sexual segregation in herbivores, but little work is done on carnivores and scavengers. I found evidence of sexual segregation in my study of the wolverines' diet. Males had a higher frequency of big game in their diet than females, and females had a higher frequency of small game in their diet than males. Segregation can be split up into two main patterns: habitat segregation and social segregation. In the case of the wolverine only habitat segregation is of interest since wolverines are solitary mammals (Banci & Harestad, 1990). There are five hypotheses that try to explain habitat segregation and these are the forage selection hypothesis, scramble competition hypothesis, predation risk hypothesis, physical conditions hypothesis and weather sensitivity hypothesis.

The predation risk hypothesis is one possible explanation of the sex difference in diet of wolverines. Females with young are often more vulnerable to predation than are adult males because they are protecting their cubs, and might therefore be more sensitive to predation risks (Lingle, 2000; Lingle & Wilson, 2001). Wielgus and Bunnell (1994) found that there was sexual segregation within the grizzly bear population in Alberta, Canada. They found that females were avoiding old forest in spring and autumn because of the possibility of encountering male bears. Male bears frequently kill bear cubs. Infanticide was the number one cause of juvenile mortality in wolverine populations in Sarek, Sweden and in Troms, Norway (Persson *et al.*, 2003), and Hornocker and Hash (1981) found that the cause of death among

four juvenile wolverines in North America, were starvation and wolf predation. It is likely that juvenile wolverines are most vulnerable when they are left unattended in the natal den (March-April) and when they just after leaving it (Landa *et al.*, 1997b). The female may avoid carrion due to the increased risk of encountering other wolverines or wolves and choose to adopt the less risky strategy of hunting small game. My results indicate sexual segregation of wolverine by diet (females ate more small game and less big game than males), which supports the predation risk hypothesis. This may suggest that females' trade off the more valuable prey for less valuable but safer prey.

One second mechanism for the sexual segregation might be that females reduce their home range during the time of denning (Banci *et al.*, 1990), and this reduction is probably a necessity of not leaving the helpless cubs in the snow cave to long at a time (Skogland, 1994). This reduced home range and the dependent cubs might limit the search for carrion. This study could not differentiate between these two possibilities.

4.3 Differences between habitats (H3)

My analyses revealed that there is no difference in wolverine diet by habitats type (forest, tundra, shrub land) but diet changes with altitude. The distribution of the wolverine is connected to the distribution of reindeer all over the northern hemisphere, from Alaska through Siberia to Scandinavia (Skogland, 1994), with reindeer mainly inhabiting tundra habitat. The tundra is usually above 1000 m a.s.l., and the tree line is also around this altitude. Moose mainly inhabit forest habitats which would include the birch belt (the highest part of the forest, around 1000 m. a.s.l). So it is as predicted that the wolverine had higher frequencies of reindeer in the diet above 1000 meters than below. Neither altitude nor habitat were significant in my model of moose in wolverine diets, likely implying that wolverines foraging in the forest may also leave their faeces in alpine habitat.

The two previous studies of wolverine diet in Norway have both identified reindeer as the most important prey making up 84.0% and 81.6% of the diet. I found that moose was more important than reindeer. Reindeer only stood for 29.1% of the diet while moose stood for 42.3%. The switch from a reindeer dominated diet to a moose dominated diet can be a result of wolf recolonization and increases in the moose population. Wolverine predation on wild reindeer has only been documented in a few cases from Snøhetta, Norway. Skogland (1994) found that the age of the female reindeer that the wolverine killed during late winter were between 10 and 13 years, the teeth were worn down, and they had been in a poor physical condition. This would indicate that wolverines are a selective hunter of old and week

individuals (Skogland, 1994), and that wolverine predation on reindeer is largely compensatory.

The NN population had a higher frequency of moose in their diet than the SS population. This supports the habitat hypothesis, because the two populations live in different habitats. The SS population inhabits mostly mountain areas while the NN population inhabits mostly in the mountain forest and in forest areas. The distribution of moose is as mentioned above, so it is as predicted that the wolverine should have larger frequency of reindeer than moose in the diet above 1000 m a.s.l and higher frequency of moose below 1000 m a.s.l. and therefore the SS population should have lover frequencies of moose in their diet than NN.

4.4 Annual variation (H4)

I found annual variation in the wolverine diet during wintertime. Deep snow causes increased energy expenditure in ungulates, resulting in weakened animals that are more vulnerable to predation (Gese *et al.*, 1996), and more animals, primary old and weak individuals, will die of starvation and exhaustion. Snow can make it easier for wolverine to catch large prey (Wilson, 1982), and therefore the hunting success during wintertime is largely influenced by the snow conditions. Snow conditions that support wolverine but not reindeer, make reindeer an easy wolverine prey item (Ewer, 1973). Haglund (1966) showed that under certain snow condition the wolverine could move much better than the red fox (*Vulpes vulpes*), who would sink deeper down into the snow than the larger wolverine, so the wolverine can move on top of the snow when other animals can not. Rausch and Pearson (1972) determined that many of the moose and reindeer the wolverine was eating was killed by wolves or hunters. Wolverine attack large animals, such as reindeer, by jumping on the back of the animal and killing it with bites to the neck (Haglund, 1966). Even if the wolverine is quite small it is known for the ability of killing grown moose that weigh 200-300 kg or more (Haglund, 1974). It is also possible that wolverines change hunting areas due to snow depth (Landa *et al.*, 1997a). With only four years of data, it is not possible to directly link annual variation in diet to variation in snow depth. Also, since my study area is so large, it is difficult to relate diet directly to the snow depth from local weather stations. However, it is well known that the North Atlantic Oscillation (NAO) is linked to snow depth at broad scales of southern Norway (Mysterud *et al.*, 2000), and this can make it possible to at least suggest whether the observed annual variation is likely related to variation in snow depth. The NAO is a large-scale alternation of atmospheric pressures (Lamb & Peppler, 1987). The fluctuations in NAO explain up to 50% of the interannual variation in wintertime precipitation over the past 72

years in Norway (Hurrell, 1995). When the NAO index is positive the wintertime temperature in Norway is high with a lot of precipitation. At low altitudes, a positive NAO index is correlated with a lot of rain. At high altitudes this increased precipitation comes mainly as snow (Mysterud *et al.*, 2000). So a high NAO index are expected to give more big game in the diet for the wolverine at high altitude, but not at low altitude, while the opposite is expected with a low NAO value. Results were not entirely consistent with the view that the snow depth predicted from the NAO can explain the annual variation in diet observed (see appendix table 2). The much higher proportion of small prey in the diet year 2002, may also suggest that abundance or availability of rodents can play a role, but this remains to be determined.

Wilmers *et al.* (2003) found that wolves appeared to reduce the variation within and between years in carcass availability. I failed to find such an interaction between annual variation and presence of wolf in the short time series available. My study did highlight that wolves can change ecosystem function in northern ecosystems. How this may interact with possible climate change remains to be determined with greater confidence.

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Appendix

Appendix table 1. Frequency of occurrence of items in faeces of wolverine in southern Norway during wintertime in the years 2001 to 2004.

	Bones				Fragments				Feathers		
	Small mammals	Large mammals	Birds	Unknown	Soft tissue	Berries	Plant	Unknown fragments	Passeriformes	Galliformes	Unknown
Females	2.33	17.18	0.61	10.43	9.45	0.00	11.04	2.58	0.12	0.491	0.368
Males	0.74	12.88	0.25	10.31	7.36	0.25	8.22	2.33	0.00	0.000	0.368
Unknown	6.01	8.96	2.21	12.03	12.15	5.15	18.90	6.38	0.25	2.577	2.209
Total	9.08	39.02	3.07	32.76	28.96	5.40	38.16	11.29	0.37	3.067	2.945

	Hair										
	Wolverine	Reindeer	Moose	Roe deer	Hare	Sheep	Rodents	Insectivora	Badger (*Meles meles*)	Unknown	Total
Females	1.718	8466	13.620	0.123	1.227	0.982	4.294	0.123	0.000	6.380	36.93
Males	0.491	8.589	11.779	0.491	0.613	0.491	2.209	0.123	0.123	4.417	29.33
Unknown	0.736	11.902	16.196	0.736	3.190	1.718	13.865	2.699	0.000	5.031	56.07
Total	2.945	28.957	41.595	1.350	5.031	3.190	20.368	2.945	0.123	15.828	

Appendix table 2. Expected changed in frequency of big game and small game in the diet above and below 1000m a.s.l. for the years 2001-2004 as predicted from the NAO index. The results are not consistent with the predictions.

	2001	2002	2003	2004
NAO	-1.89	0.76	0.20	-0.07
Above 1000	Big game – small game +	Big game + small game -	Big game + small game -	Big game – small game +
Below 1000	Big game + small game -	Big game – small game +	Big game – small game +	Big game + small game -